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The Freshwater Eels
(*Anguilla* spp.)
of Southern Africa.
An introduction to
their identification and
Biology.

SUMMARY

Five species of freshwater eels have been found in the rivers of South Africa, *Anguilla marmorata* Quoy and Gaimard, 1824, *Anguilla nebulosa labiata* Peters, 1852, *Anguilla mossambica* Peters, 1852, *Anguilla obscura* Gunther, 1871, and *Anguilla bicolor bicolor* McClelland, 1844. These are described and a simplified key provided for their identification.

The distribution of the two predominant species *A. nebulosa labiata* and *A. mossambica* is associated with zones on the African coast where elvers of these species reach the river mouths: between the equator and 21 S. in the case of the former, and between 21 S. and 32 S. in the case of the latter species. The dispersal of these two species over a river system appears to be governed by the size of the eel reaching the river mouth and not by water temperature or any particular environment. Distribution outside these elver zones is carried out at sea by post-elvers, and a considerable wandering along the coastal shelf takes place.

Elvers of *A. mossambica* reach the Natal coast in January, and those of *A. nebulosa labiata* and *A. bicolor bicolor* have been reported from the coast of East Africa in January and February. Mature silver male and female *A. mossambica* leave the South African rivers during the period November to March, during which period mature silver female *A. marmorata*, *A. nebulosa labiata* and *A. bicolor bicolor* have also been discovered. Secondary migrations by post-elvers up the rivers of the South-east Cape and Natal are observed during the period January to April.

A length-weight curve for the material on hand is provided, also a histogram showing the change of feeding habits with increase in size.

A hypothetical breeding place for the eels of the West Indian Ocean is discussed in relation to the sea currents of this area, and an indirect route possibly taken by post-elvers reaching the south-east and south coast rivers described.

The economic exploitation of eel populations is discussed briefly, and it is pointed out that whilst the annual supply of elvers from the sea is a permanent natural resource, the exploitation of eel populations from these elvers is related to the permanency and availability of inland waters.

THE FRESHWATER EELS (*ANGUILLA* SPP.) OF SOUTHERN AFRICA.
AN INTRODUCTION TO THEIR IDENTIFICATION AND BIOLOGY

Up to only three years ago relatively little was known about the freshwater eels of Southern Africa. Scarcely any biological or ecological investigations of note had been carried out.

and the systematic picture had been obscured by the opinions of remote authorities. For these reasons, when I joined the Department of Ichthyology at Rhodes University, Professor J. L. B. Smith suggested the investigation of the eels as my first assignment. The results set out below summarise the advances in knowledge that have resulted, and the position to date.

The first work of any note on the freshwater eels of the area of the Western Indian Ocean was done by Peters (1), who, in 1852, described four species of freshwater eels from Portuguese East Africa. These were two mottled eels *Muraena* (*Anguilla*) *macrophthalmia* and *Muraena* (*Anguilla*) *labiata*, a plain long-finned eel *Muraena* (*Anguilla*) *mossambica*, and a plain short-finned eel *Muraena* (*Anguilla*) *virescens*. *M. (Anguilla) macrophthalmia* has since proved to be the mature male of the species *M. (Anguilla) labiata*. Subsequent to this other workers named varieties of mottled eels and plain eels from the Indian Ocean, and by the time Gilchrist and Thompson (2) published their work in 1917, there was considerable confusion about the species found in the rivers of Southern Africa. These two authors recognised Peter's *Anguilla mossambica*, but assigned *M. (Anguilla) labiata* and *M. (Anguilla) macrophthalmia* to *Anguilla bengalensis* Gray, 1830, and the short-finned eel *M. (Anguilla) virescens* to *Anguilla australis* Richards, 1841. Further confusion arose when the late Professor J. Schmidt, who had initiated a world-wide investigation into the biology of the freshwater eels, examined a number of specimens of South African eels and stated that they were all of one species, *Anguilla mossambica*.

Dr. Vilh Ege carried on with Schmidt's work, and his "Revision of the Genus *Anguilla* Shaw" (3), published in 1939, placed the systematics of the freshwater eels of the world on a sound basis. In addition to collecting and examining fresh material Ege was able to examine all existing types, and the final outcome of this classic research was the reduction of 70 described species to a total of 16.

The freshwater eels were divided into four distinct groups:—

- (1) Species with mottled skin pattern and long dorsal fin, and in which the maxillary teeth are in several rows close together.
- (2) Species with mottled skin pattern and long dorsal fin, and in which the maxillary teeth have a distinct longitudinal groove.
- (3) Species with plain unmottled skin and long dorsal fin.
- (4) Species with plain unmottled skin and short dorsal fin.

These groups, which must refer to specimens of greater than 20 cm. in length, were subdivided principally on dimensions, dentition and vertebral counts. As shown in figure 1, the important dimensions are the pre-anal (A), pre-dorsal (D), length of head (E), and the total length (L) of the eel. These are measured as shown in figure 1 and the ano-dorsal distance (A—D) is expressed as a percentage of the total length L. Thus long-finned eels give average values of 10 to 20 per cent, and short-finned eels values of 3 to 5 per cent. The negative values signify that the dorsal fin originates behind the vertical through the anus.



Fig. 1. Dimensions of Eel

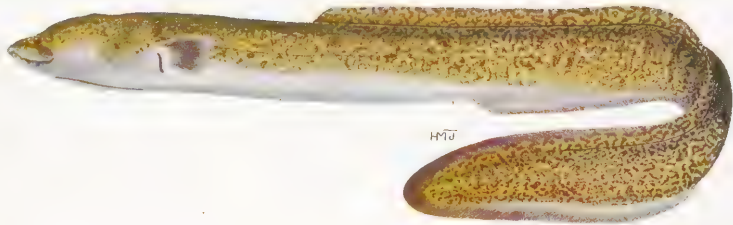


PLATE I

Anguilla nebulosa lobata Peters, 1952.
African Mottled Eel, Specimen (108 cm.) taken in the Umzimkulwana River, Natal.

Based on Ege's detailed characteristics five species of eels have been found in the rivers of South Africa (4), (5), (6). These can be assigned to the broad groups 2, 3 and 4 above. A simplified key for their identification would be as follows:—

Key to the Species of *Anguilla* found in South African Rivers.

A. Specimens of 20 cm. total length and over:—

1. Distinct mottled skin pattern on dorsal surface, extending to ventral surface posterior of the anus; mottled skin pattern dark and diffuse on dorsal surface in very large specimens; dorsal fin long; maxillary teeth with distinct longitudinal groove.

- 1.1. Ano-dorsal length 14 to 19 per cent of total length (fig. 9); vertebral count 103 to 108 (fig. 2); longitudinal groove in maxillary teeth extends to posterior end of band (fig. 4).

Anguilla marmorata Quoy & Gaimard, 1824.

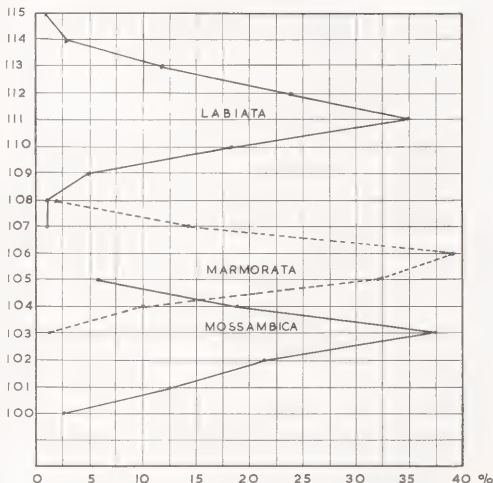


Fig. 2. Percentage frequency of total number of vertebrae. (After Jespersen).

- 1.2. Ano-dorsal length 7 to 15 per cent of the total length (fig. 9); vertebral count 107 to 115 (fig. 2); longitudinal groove in maxillary teeth does not extend to hindermost tip of band (fig. 5). *Anguilla nebulosa labiata* Peters, 1852.
2. Skin without mottled pattern; maxillary bands of teeth in several rows and without longitudinal groove (fig. 6).
- 2.1. Ano-dorsal distance 9 to 17 per cent of the total length (fig. 9); vertebral count 100 to 105 (fig. 2). *Anguilla mossambica* Peters, 1852.
- 2.2. Ano-dorsal length 1 to 5 per cent of the total length; vertebral count 102 to 107 (fig. 3); length of intermaxillary-vomerine band of teeth 70 to 80 per cent of the length from the front end of this band to the posterior tip of the right maxillary band (fig. 7). *Anguilla obscura* Gunther, 1871.

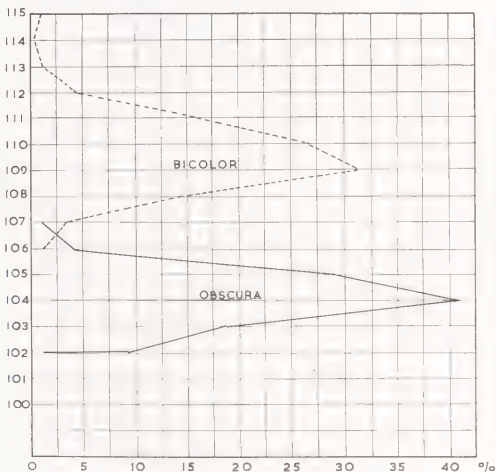


Fig. 3. Percentage frequency of total number of vertebrae. (After Jespersen)

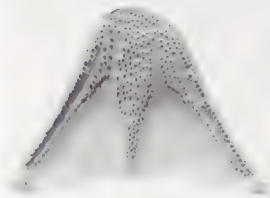


Fig. 4. *Dentition A. marmorata*

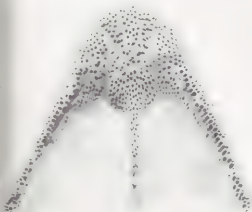


Fig. 5. *Dentition A. nebulosa labiata*

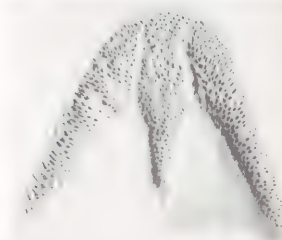


Fig. 6. *Dentition A. mossambica*

2.3. Ano-dorsal distance -1 to $+3$ per cent of the total length; vertebral count 106 to 115 (fig. 3); maxillary band of teeth broad; length of intermaxillary-vomerine band of teeth 85 to 95 per cent of the length from the front end of this band to the posterior tip of the right maxillary band (fig. 8). *Anguilla bicolor bicolor* McClelland, 1844.

B. Specimens of less than 20 cm. in length:—

In the case of small eels the dentition is not fully developed, and the mottled pattern difficult to discern in eels of less than 15 cm. What pattern there is is in the form of blotches rather than a distinct pattern. It is possible to separate the long-finned eels from the short-finned

eels by the ano-dorsal values. It would also be possible to separate young of *A. marmorata* from those of *A. nebulosa labiata* by the ano-dorsal values, but where dentition and skin pattern cannot be used, as in the case of very small eels, the presence of young of *A. mossambica* would confuse the issue. This is shown in fig. 9. In this investigation the identification of small specimens has been carried out by sorting the material into extremes of ano-dorsal values, dissecting, staining with alizarine, clearing and counting the vertebrae with the aid of a microscope. Only in the case of *A. mossambica* was there abundant material, so the use of the pigment pattern on the caudal could not be used with any confidence to detect specimens of the other long-finned species from a batch of small eels.



Fig. 7. Dentition *A. obscura*

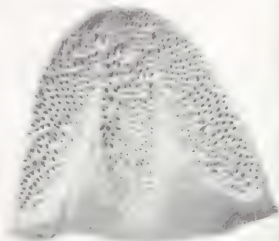


Fig. 8. Dentition *A. bicolor bicolor*

DESCRIPTIONS

Anguilla marmorata Quoy & Gaimard, 1824.

Common names: Mottled eel, Conger eel (Eastern Cape), Geelbonte paling, Swartwitpens paling.

Ege records the following synonyms:—

A. mauritiana Bennett, 1831. *A. labrosa* Richardson, 1844. *Muraena maculata* Bleeker, 1864. *Muraena mamillensis* Bleeker, 1864. *Anguilla johannae* Playfair & Gunther, 1866. *Anguilla fulgens* Gunther, 1870. *Anguilla huldebrandti* Sauvage, 1891. *Anguilla bengalensis* Reuvsen, 1895.

A. marmorata is an Indo-Pacific species with a very wide distribution in the west Indian Ocean. The first specimens of this species to be examined during this investigation came from the Kaffrarian Museum (7), but later specimens were collected in the Sundays River, the Buffalo River, and the Sabi-Lundi River system, Southern Rhodesia (8). Material in the South African Museum came from the Bashee River, Transkei. Frost (9) reports a specimen of 127.0 cm. from the Lusumfwa River, Zambezi River system. Altogether 17 specimens

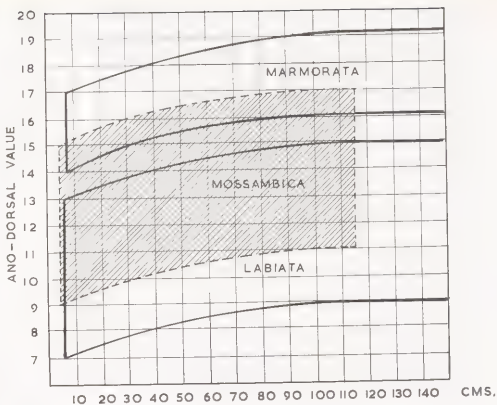


Fig. 9. Block diagram enclosing scatter points for values of anodorsal distance, expressed as a percentage of total length, for *A. marmorata*, *A. nebulosa labiata* and *A. mossambica*. This diagram shows how values for *A. mossambica* overlap, for all ranges in size, those of the other two long-finned eels.

have been examined covering a range of 17.7 cm. to 134.0 cm. in length. Some very heavy mottled eels have been caught by anglers in the Keiskama River, and the Transkei rivers, and weights of up to 45 lb. claimed. Very large eels are also caught in the lowveld rivers of Natal and the Eastern Transvaal. From photographs examined these would be either *A. marmorata* or the next species, *A. nebulosa labiata*; both species attain 183.0 cm. in length.

Although very similar, the colour pattern of *A. marmorata* is not as bold as that of *A. nebulosa labiata*. (fig. 10 and fig. 11.) *A. marmorata* has a mottled pattern of dark brown-green on a background of olive-yellow which extends from the top of the head anteriorly and covers the whole body posterior of the anus, pronounced in the dorsal fin but faint in the anal fin, the belly is pale yellow. A mature female eel of this species, which was taken in the Sundays River at Addo, was nearly uniformly dark brown-green on the dorsal surface with a silvery pink belly, the mottled pattern was only evident on the sides of the head and body. This particular specimen was recognised by an experienced eel angler of Addo by the common name of swartwitpens paling, the black white-bellied eel.

As indicated in fig. 9 the ano-dorsal values cover a range of 14 to 19 per cent of the total



Fig. 10. Skin pattern *A. marmorata*



Fig. 11. Skin pattern *A. nebulosa labiata*

length with a tendency to increase with the size of the eel. The vertebral counts of six specimens gave a range of 105 to 106. Dentition patterns were taken of all specimens, using plasticine. These showed quite clearly the distinct longitudinal groove in the maxillary teeth bands. The pattern shown in fig. 4 is typical of the specimens examined.

No male specimens of *A. marmorata* have been found during this investigation; of those which could be sexed all have been found to be females.

South of the Limpopo River *A. marmorata* is confined to the deep pools of flowing

rivers above the ebb and flow and some 10 to 50 miles inland. The largest specimens are taken by anglers at, or near, the ebb and flow, and occasional specimens are taken in the tidal sections of these rivers. In Southern Rhodesia *A. marmorata* was taken 230 miles inland by river from the sea; the specimen reported by Frost (9) was taken approximately 600 miles inland.

***Anguilla nebulosa labiata* Peters, 1852. (Plate I.)**

Common names: Mottled eel, Conger eel (East Cape), Geelbonte paling.

Synonyms:—

Muraena (Anguilla) macrophthalma Peters, 1852.

As will be seen from the common names this eel is generally confused with the previous species, *A. marmorata*. The mottled pattern is, however, bolder than that of *A. marmorata*. In specimens taken from muddy water the colouring is much lighter and the background colour yellow; those taken from deep rocky pools with clear water have been found to be very dark but with distinct mottled pattern. A mature female from the Loskop Dam, Olifants River, Transvaal, forwarded by the Lydenburg Fisheries Institute was uniformly very dark on the dorsal surface with mottling on sides. In specimens of 13 cm. collected in the lower Lundi River, Southern Rhodesia the mottling was discernible as a blotchy pattern.

Altogether 47 specimens were collected and examined, and these, together with the dimensions of 63 kindly forwarded by Dr. Frost, 3 presented by R. Bolt, and the statistics of 119 extracted from Ege, give an ano-dorsal distance range of 7 to 15 per cent of the total length, with a peak frequency range of 11 to 13 per cent. As shown in fig. 9 these ano-dorsal values overlap those of *A. mossambica*, but elvers and small post-elvers can be separated positively by vertebral counts.

Vertebral counts made from fresh material fell between the range 109 to 112. The dentition pattern is very similar to that of *A. marmorata*, and the termination of the longitudinal groove posteriorly in the maxillary teeth is not always as clearly defined as in fig. 5. In specimens less than 16 cm. in length it has not been possible to determine the dentition pattern with confidence.

No male specimen of this species has been found in South African rivers. A mature male of 59 cm. was presented by R. Bolt; this was collected near Chirundu, Zambezi River, during September 1959.

Frost (10) has shown that *A. nebulosa labiata* is the predominant species of eel in the rivers of Kenya. This author found the same to be the case when examining eels from Northern Rhodesia (9). It is the only species reported from Lake Nyasa (11) and the trout streams of the Inyanga Mountains, Southern Rhodesia (12). Field work in this latter area showed this to be the case in the Gairezi River, Zambezi system, and the Pungwe River. South of this area the distribution of *A. nebulosa labiata* extends southwards along the coast and round to as far west as Knysna, but as we come southwards the numbers decrease and this eel is found nearer and nearer to the sea. West of Knysna occasional mottled eels are reported from the lower reaches of the Goukamma and Breede Rivers; these may be *A. nebulosa labiata*, or the previous species *A. marmorata*.

***Anguilla mossambica* Peters, 1852.**

Common names: Plain long-finned eel. Black eel. Rock eel. Paling. Geelbek paling (South-Western Cape). Swart paling.

Synonyms:—

Anguilla delalandi Kaup, 1856. *Anguilla capensis* Kaup, 1859.

This is the common eel of South African rivers. The colour varies from a uniform slate to dark chocolate-brown on the dorsal surface, extending to the whole body posteriorly, lighter on sides, with silvery yellow belly. Mature eels have a very dark bronze dorsal surface

and sides, with silvery iridescent pink belly. Excluding true elvers, 1,454 specimens were examined covering a range of 8.7 cm. to 122 cm. in length. The heaviest eel of this species examined during this investigation weighed 10 lb. 8 oz.; the more common weight was 5 to 7 lb. Where free to move up or downstream, *A. mossambica* is undoubtedly a much smaller eel than either of the two mottled eels *A. marmorata* or *A. nebulosa labiata* and records of weights in excess of 20 lb. are almost certainly due to a misidentification of the species.

The ano-dorsal distances had a range of 9 to 17 per cent of the total length (fig. 9). The dentition pattern (fig. 6) is quite distinct from that of the other two long-finned eels. Samples covering the whole distribution range in southern Africa were dissected for vertebral counts and these gave a range of 100 to 104.

Field work has shown that *A. mossambica* is the predominant eel from the Sabi-Lundi River system in Southern Rhodesia, southwards to the south coast and as far west as Knysna. West of Knysna the numbers decrease, the Breede River being the furthest west where it is found in fair numbers. Occasional specimens are reported from the vicinity of Cape Town.

Material examined in the South African Museum included a large *A. mossambica*, S.A.M. 12761, from the confluence of the Caledon and Orange Rivers. The McGregor Memorial Museum, Kimberley, has another specimen taken from the Vaal River near that town (13). For reasons to be discussed later, it is considered that these occasional *A. mossambica* that enter the Orange River system, do so by an overland route from the Limpopo River system.

***Anguilla obscura* Gunther, 1871.**

A single specimen of 35.5 cm., which has been assigned to this species, was collected in a tributary of the Buffalo River, near King William's Town, on the 8th of August, 1957 (5). Being a short-finned eel it was easily separated from the *A. mossambica* collected at the same time. Being very dark in colour this eel was examined critically. The dentition pattern (fig. 7) differed greatly from that of the better-known *A. bicolor bicolor* (fig. 8), the length of the intermaxillary-vomerine band of teeth being 73 per cent of the distance from the front margin of that band to the posterior end of the right maxillary band. The ano-dorsal distance was 2.4 per cent of the total length, and the vertebral count 103. In direct comparison there is a very great difference in colour between this specimen and specimens of *A. bicolor bicolor*; the former is generally dark slate with lighter belly, and the latter are olive-grey. The gonads were not sufficiently developed to determine the sex with any certainty.

As this was the first record of this species in the Indian Ocean a careful search has been made for additional specimens, but, to date, none has been found.

***Anguilla bicolor bicolor* McClelland, 1844.**

Common name: Short-finned eel.

Synonyms:—

Muraena (*Anguilla*) *virescens* Peters, 1852. *Anguilla dussumieri* Kaup, 1856. *Anguilla cantori* Kaup, 1856. *Anguilla amblodon* Playfair & Gunther, 1866. In the works of Boulenger 1915, and Gilchrist & Thompson 1917, this species has been referred to as *Anguilla australis* Richardson, 1841.

This eel is widely distributed over the Indian Ocean, and along the coast of Africa; although not common, it has been collected from Knysna to the Sabi-Lundi River system in Southern Rhodesia. Frost (10), (14) reports this species from the rivers of Kenya. In South Africa and in Kenya *A. bicolor bicolor* has been found near the sea, but it is interesting to record that 4 specimens were collected in the Lundi River, Southern Rhodesia, in May 1958, at a site 190 miles by river from the sea, altitude approximately 900 feet.

The material examined covers two specimens, 58.0 and 60.0 cm. in length from the Seychelles, a single specimen from Zanzibar Island 62.0 cm. in length, all collected by Prof.

J. L. B. Smith, a specimen of 64.0 cm. from Zululand presented by Mr. L. van Heerden, 4 forwarded by the Kaffrarian Museum, and 10 collected during field work. A live specimen in the aquarium of the Lydenburg Provincial Fisheries Institute has been inspected. In colour, this latter specimen, like Mr. van Heerden's, has the dark colour of an eel approaching maturity. Preserved specimens are light olive-brown in colour with a very light belly. Live specimens were olive with very light underparts.

Anguilla bicolor bicolor is easily recognised by its short dorsal fin; the ano-dorsal distance, in the material on hand, is 0 to 1 per cent of the total length. The broad bands of the maxillary teeth are quite different from the maxillary teeth of the specimen assigned to *A. obscura*, this can be seen by comparing fig. 7 and fig. 8. The length of the intermaxillary-vomerine band of teeth is 90 to 95 per cent of the distance from the front margin of that band to the posterior end of the right maxillary band. Vertebral counts gave values of 108 to 110.

Of those specimens which could be sexed, all were females. The Zululand specimen of 64.0 cm., 1 lb. 1 oz. in weight, is a mature female with large gonads.

Anguilla anguilla Linnaeus, 1758.

Although not included in the key for South African species of *Anguilla*, mention must be made here of the fact that Ege (3) records 6 specimens of *A. anguilla* from East Africa, exact locality unknown, and three specimens from Nairobi, again exact locality unknown. Similar in general appearance and dentition to *A. mossambica*, *A. anguilla* has a vertebral count which averages 115 and falls within the range of 110 to 119, well beyond the limits of the vertebral count for *A. mossambica*. Frost (10) obtained no specimens of *A. anguilla* in Kenya, and no specimens of *Anguilla* have been found in South African rivers which can be assigned to this species. It is, however, essential to examine critically those eels resembling *A. mossambica* and having a very low ano-dorsal distance.

LIFE HISTORY OF THE EUROPEAN EEL, *Anguilla anguilla*

Due to its great economic importance in western Europe, a considerable amount of research work has been carried out and published on the life history of the European eel, *Anguilla anguilla*. Based on the researches of the famous Danish oceanographer, the late Professor Johannes Schmidt, Bertin (15) has summarised the life history of *A. anguilla* as follows:—

- (a) Marine larval phase, or phase of dispersal lasting two or three years.
- (b) First metamorphosis, leptocephalus into elver.
- (c) Phase of growth in fresh water, lasting 8 to 18 years, the yellow eel.
- (d) Second metamorphosis, yellow eel into silver eel, migration to the sea.
- (e) Adult marine phase, or phase of reproduction, of unknown duration.

From the study of the marine larval stages Schmidt located a spawning area for *A. anguilla* in the centre of the Sargasso Sea. In piecing together the evidence at his disposal Schmidt had to contend with two problems—the spectacular migration of some 3,500 miles by mature eels from the rivers of Europe and North Africa to this spawning area, and the fact that the North American eel, *A. rostrata*, also appeared to spawn in the same region. Schmidt then came to the conclusion that the duration of pelagic life during marine dispersal was finally responsible for separating the species. These two eels are very similar in characteristics until we come to the vertebral count, in *A. rostrata* the vertebral count ranges from 103 to 111, and in *A. anguilla* it is 110 to 119.

Dr. D. W. Tucker (16), (17) has re-examined all available evidence regarding the life history of these two eels and has propounded a theory of his own. In brief, Tucker considers that the European silver eel is too degenerate to complete the long migration back to the spawning area in the Sargasso Sea, and that the North American eel is in a much better condition to carry out the shorter migration required of it. He then assumes, with qualifying

evidence, that the European eel, *A. anguilla*, and the North American eel, *A. rostrata*, are one and the same species, and attributes the difference in vertebral count to larval environment, the larvae having originated from American parents.

LIFE HISTORY OF SOUTH AFRICAN EELS

There is sufficient evidence from this investigation and the published results of other research workers, to show that the five important phases in the life history of *A. anguilla* are applicable to the species of *Anguilla* found in the rivers of southern Africa. As these species can be separated by other characteristics as well as vertebral counts, and as there are hypothetical breeding grounds within reasonable reach, Tucker's new theory does not affect the issue directly.

MARINE LARVAL PHASE

During the cruise of the "Dana" in the western Indian Ocean, mid-December 1929 to mid-January 1930, *Anguilla* larvae were collected in the Mozambique Channel, and between the northern tip of Madagascar and the coast of East Africa. These have been described by Jespersen (18) as larvae of *A. marmorata*, *A. mossambica* and *A. bicolor bicolor*. (See fig. 25.) From investigations carried out in the eastern Indian Ocean Jespersen concluded that the pelagic life of *A. marmorata* and *A. bicolor bicolor* was a short one, and that several spawning places in the Indo-Pacific Ocean were involved.

METAMORPHOSIS, LEPTOCEPHALUS INTO ELVER

Jespersen (18) also described one metamorphosing stage and one glass eel from the Mozambique Channel taken on the 10th January, 1930 and identified as *A. mossambica*. At the same time Jespersen drew attention to how much more advanced these larvae of *A. mossambica* were in comparison with larvae of *A. marmorata*, taken just prior to this off the northern tip of Madagascar.

Skead's observations of upstream migrating eels at the wall of the Laing Dam, King William's Town, started in the summer months of 1955 and since that date scientific records have been consistently maintained (19), (20), (21), (22), (23), (24). Material collected during these observations was generously presented to this Department. Although collected within 25 miles by river from the sea, the discrepancy in size between these young eels, which had the characteristics of migrating elvers, and the true elvers of *A. mossambica*, 46 mm. to 56 mm. in length, recorded by Ege (3) from Madagascar, became apparent. (See fig. 12.) As the bulk of the Laing Dam material proved to be one species, *A. mossambica*, a search was made in the rivers of the Eastern Cape for young eels of comparable size. Skead extended his own observations to the wall of the East London Municipal Pumping Station on the Buffalo River, a short distance above the ebb and flow of the tidal section. Here the smallest specimen collected was 89 mm.

The first record of an elver of *A. mossambica* from a river in South Africa is that of Barnard (25). No date is given for the collection of this specimen, S.A.M. 18487, of 49 mm. with 103 myomeres, and which came from the Uvongo River. Further evidence came from Natal when in 1957 three specimens of *A. mossambica*, 51 mm. to 55 mm., came from the Provincial Fish Hatchery on the Ugeni River, approximately 40 miles from the sea. That same year, therefore, a tour was made of the Natal coast and much publicity given to this investigation. The result was that Mr. E. Drower, Warden of the Oribi Gorge Nature Reserve, discovered that Mr. T. Larkin, an annual visitor to Uvongo, had witnessed a migration of baby eels up the Uvongo River waterfalls early in January 1957. The site was visited and found to be ideal in that the Uvongo River waterfalls emptied into a rock-bound tidal estuary barely 150 yards from the sea. The co-operation of these two gentlemen was enlisted and during the first week in January 1958 and again in January 1959 migrations of elvers were intercepted and considerable material collected. These elvers can be regarded as not having spent any

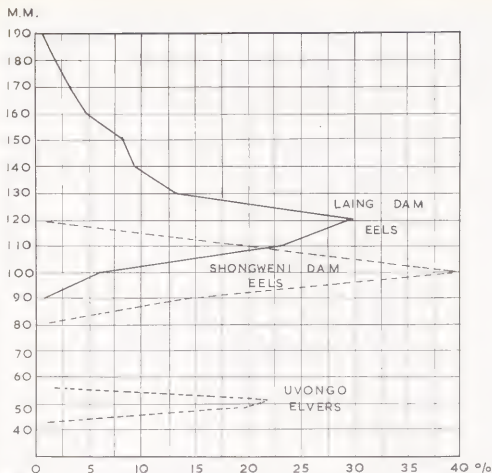


Fig 12 Percentage frequency of length of elvers of *A. massambica* from Uvongo River mouth, and post-elvers from Laing Dam and Shongweni Dam

time in fresh water, and as having come straight from the sea.

A characteristic of the young migrating eels from Laing Dam is their lack of pigment, in fact, on Strubberg's (26) specification they could be regarded as elvers in the last stages of metamorphosis. This lack of pigment is also consistent with the possibility that these eels had been at sea in relatively cold water for a long period (26), and they will be referred to as post-elvers.

The Uvongo specimens are, however, true elvers and the 1958 material could be divided into two groups:—

- those quite opaque, 45 mm. to 54 mm. in length, with a girth of 2.0 to 2.5 mm. and an average wet weight of 0.120 gram;
- those which were mostly transparent threads, 43 mm. to 53 mm. in length and an average weight of 0.105 gram; the average weight of 5 emaciated specimens was as low as 0.074 gram.

In the more transparent elvers the cranial pigment stood out clearly (fig. 13), as did the vertebrae, liver and stomach contents. Superficial pigment along the dorsal surface, combined with subcutaneous pigment along the vertebral column, gave these otherwise transparent elvers a dark appearance. In many the stomachs contained larval shrimps whose salmon pink exoskeletons and black eyes showed through the distended stomach walls and skin quite clearly. Dr. K. H. Barnard very kindly identified specimens of these as larvae of the freshwater shrimp, *Caradina nilotica*. In some of the transparent elvers remnants of the larval teeth could still be seen under a microscope. The 1959 material was preserved in alcohol and could not be fitted to Strubberg's classification with any certainty, but both emaciated and plump elvers were present. In size range there is good agreement with Ege's record (3) of elvers of *A. mossambica* from Madagascar. Of the 551 specimens from Uvongo, none could be identified as being of any other species but *A. mossambica*. Another 16 specimens from the river above the Uvongo waterfalls were received from the Natal Museum, these were collected during the 1959 migration. The 1957, 1958 and 1959 migrations at Uvongo took place during the high spring tides, two with a new moon and one with a full moon.

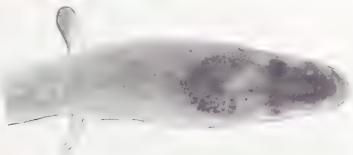


Fig. 13. Head of an elver of *A. mossambica* X 10 showing cranium pigment

Field work in Natal on the Umzimkulwana and Umlaas Rivers showed that young eels, of 70 mm. to 75 mm. in length, could be found 15 to 20 miles by river from the sea during the months August and September. These sizes were consistent with elvers of *A. mossambica* having entered these rivers during the past summer months. A complete search was made in the Kariega, Sundays and Kromme Rivers, all with mouths open to the sea, for young eels relative in size to those found in Natal, but none was found. Using the same collecting methods no small eels were found in the rivers around George, a tributary of the Kafferkuijs River, the Duivenhoek, Breede and Palmiet Rivers. A visit was also paid to the famous tame eels of Platbos, Stilbaai, at the mouth of the Kafferkuijs River (39). Here, since 1814, the de Jager family have fed eels which live in a never-failing fountain practically at the back door of the old Homestead. This fountain issues from under an outcrop of limestone filling a small shallow pool, and then flows into the tidal section of the Kafferkuijs River 400 yards away, barely the same distance from the sea. The eels live underground and come out for food. A large *A. mossambica* of about 100 cm. came out into the bright sunlight for a crab which was dangled in the pool. Mrs. de Jager explained that the large eels disappear after many years, and that about nine eels were in the fountain ranging in size down to approximately 20.0 cm. She could not recall ever having seen anything smaller, nor could the oldest surviving member of the family.

South African Museum Specimen No. 19851, which is a pigmented and plump elver of *A. mossambica*, 51 mm. in length and which came from Malagas near the ebb and flow of the Breede River, stands unique and important as the only specimen of *A. mossambica*, or any other species of freshwater eel, from the south Cape coast less than 92 mm. in length.

In mid-February 1959, Mr. M. H. Byrne of the Durban Waterworks, Shongweni Dam, Umlaas River, supplied evidence of mass migrations by pigmented baby eels smaller than the post-elvers reaching the Laing Dam wall. These migrations have been known for some many years (27) but Mr. Byrne could not remember ever having seen, stranded or migrating, any young eels as small as the Uvongo elvers. The differences in sizes between the Laing Dam post-elvers, the Shongweni Dam pigmented baby eels and the Uvongo elvers is clearly shown in fig. 12. These secondary migrations, which take place during February and March, even whilst the spillway is floodlit (27), are probably due to population pressure caused by the elvers coming in from the sea, and occupying the lower section of the river. This second migration, the following season, could explain the migrations observed at the Laing Dam wall, but, in spite of careful and routine observations by Skead and this Department on the Buffalo, Kowie and Kariega Rivers, all open to the sea, no eels less than 89 mm. have been found.

Supported by other specimens relative in size, the following is a list of the smallest eels collected or examined, with an approximate distance of the site by river from the sea:

Breede River, Malagas, 15 miles, S.A.M. 19851	..	..	..	..	..	51 mm.
Homtini River, Knysna, 20 miles	..	..	..	..	..	159 mm.
Kromme River, Churchill Dam, 18 miles	..	..	..	..	..	97 mm.
Van Staadens River, 6 miles	..	..	..	..	..	166 mm.
Swartkops River, Bulk Dam, 25 miles	..	..	..	..	..	140 mm.
Sundays River, Addo, 15 miles	..	..	..	..	..	92 mm.
Sundays River, Lake Mentz, 65 miles	..	..	..	..	..	112 mm.
Bushmans River, Eastern Cape, 26 miles	..	..	..	..	..	98 mm.
Kariega River, Howiesons Poort, 26 miles	..	..	..	..	..	126 mm.
Buffalo River, Pumping Station, $\frac{1}{2}$ mile	..	..	..	..	..	89 mm.
Buffalo River, Laing Dam, 25 miles	..	..	..	..	..	99 mm.
Kei River, Kabusie, 75 miles	..	..	..	..	..	138 mm.
Uvongo River, Uvongo Falls, $\frac{1}{2}$ mile, elver	..	..	..	..	..	43 mm.
Umzimkulwana River, Oribi, 15 miles	..	..	..	..	..	75 mm.
Umlaas River, Shongweni Dam, 20 miles	..	..	..	..	..	70 mm.
Umgeni Hatchery, Umgeni River, 35 miles	..	..	..	..	..	51 mm.
Lundi River, Southern Rhodesia, 190 miles	..	..	..	..	..	72 mm.
Lundi River, Gwenora Dam, 475 miles	..	..	..	..	..	87 mm.

All the above were identified as *A. mossambica*. Of the other species no elvers were discovered and the smallest specimens were:

Knysna River, ebb and flow, <i>A. bicolor bicolor</i>	..	..	..	..	..	121 mm.
Kromme River, Churchill Dam, 18 miles, <i>A. nebulosa labiata</i>	..	..	..	..	..	176 mm.
Buffalo River, Laing Dam, 25 miles, <i>A. marmorata</i>	..	..	..	..	..	174 mm.
Lundi River, Southern Rhodesia, 190 miles, <i>A. bicolor bicolor</i>	..	..	..	..	..	149 mm.
Lundi River, Southern Rhodesia, 190 miles, <i>A. nebulosa labiata</i>	..	..	..	..	..	90 mm.

Frost (14) was the first to describe elvers of *A. nebulosa labiata*, specimens of 54.0 and 58 mm., from the Mzingu River near Dar-es-Salaam, as well as elvers of *A. bicolor bicolor* from the same site. These latter elvers were 50.0 to 61.5 mm. in length, and all were collected during the period late January to mid-February 1956. Whitehead (28) reports specimens of *A. nebulosa labiata* 104.0 to 161.0 mm., taken in the Tana River during April 1958 at a site 350 miles by river from the sea. These could have been elvers of the 1957 migrations.

From the discussion above it is evident that, in the case of *A. mossambica*, metamorphosis takes place off the east coast of Africa between 21° S. and 31° S., and elvers reach the river mouths falling within this zone. Those post-elvers reaching the Buffalo River and other rivers of the south-east and south Cape coast do so by carrying out a secondary migration. From their length these post-elvers are a year to a year and a half older than the elvers, and even more in the case of larger specimens. Migrations of elvers take place in South Africa and Madagascar during the period January to March with maximum activity during January and February. The migrations of post-elvers at the Laing Dam wall, as recorded by Shead (24), take place during the period January to April.

PHASE OF GROWTH IN FRESH WATER. THE YELLOW EEL

DISTRIBUTION OVER A RIVER SYSTEM

The two predominant eels found in southern Africa are *A. nebulosa labiata* and *A. mossambica* (fig. 14). The inland distribution of these eels is of considerable interest as it points to a critical size at which the eel either loses its desire to migrate inland or is not capable of negotiating an obstruction.

Dealing first with *A. nebulosa labiata*, Frost (10) found three species of eels in the easterly flowing rivers of Kenya, *A. nebulosa labiata*, *A. mossambica* and *A. bicolor bicolor*, and of these the former was the only species found in the rivers above 3,000 feet, and the trout streams of the highlands. Van Someren and Whitehead (28) confirmed this in a later paper. In the trout waters of the Inyanga Mountains, Southern Rhodesia, and above broken waterfalls totalling nearly 1,000 feet, Turnbull-Kemp (12) has found just one species *A. nebulosa labiata*. Field work carried out in this same area in 1958 resulted in the same species being found in the Gairezi River, Zambezi River system, and the Pungwe River. From Northern Rhodesia Frost (9) has reported *A. nebulosa labiata* from above the Lusemwa Falls. These falls, which total 200 feet, are on the Lusemwa River which belongs to the Zambezi system, and approximately 630 miles by river from the sea. The Shire River, the only outlet to Lake Nyasa, flows down waterfalls and cataracts for a distance of 30 miles and a drop of 1,000 feet before joining the Lower Shire and finally the Zambezi River. This cataract section of the Shire River has isolated the fish fauna of Lake Nyasa from that of the Zambezi River for a long period in the geological history of the lake, a period of time sufficient for the evolution of 185 endemic species, but it has not stopped *A. nebulosa labiata* from entering the lake (11), (43).

South of the Pungwe River which rises in the Inyanga highlands, we find the Sabi River which is fed by the Lundi River, both systems rising on the Southern Rhodesia plateau at an altitude of between 4,600 and 5,000 feet. Field work at the headwaters of the Lundi River at 4,600 feet and 475 miles from the sea, revealed the presence of one species of eel, *A. mossambica*. As rotenone was used extensively in this area for collecting it is unlikely that other species would have escaped detection. In the Umshandige Dam on a tributary of the Tokwe River, also of the Lundi system, *A. mossambica* was the only species collected. However, below the 80-foot high spillway, which is approximately 375 miles from the sea, out of a total of 47 eels taken by rotenone, seven were large *A. nebulosa labiata* and the rest *A. mossambica*. In the Limpopo River system, *A. mossambica* was found to be the only species from the highveld, but *A. nebulosa labiata* was common in the lowveld section of the Nuanetsi River. In the Transvaal specimens of eels from the trout streams of the Haenert/berg have all been *A. mossambica*, whereas specimens from Marble Hall and the lowveld have been both this species and *A. nebulosa labiata*. Through Natal southwards the predominant eel throughout the system is *A. mossambica* with occasional *A. nebulosa labiata* found in the lower reaches and near the sea.

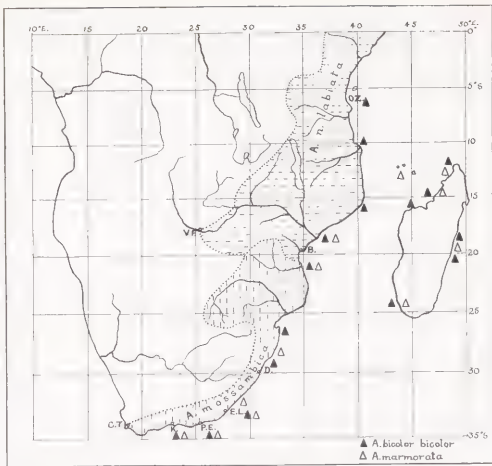


Fig. 14. Distribution of the four species of freshwater eels found in Southern Africa. The predominant eels are *Anguilla mossambica* in the south and *A. nebulosa labiata* in the north—each of these extends into the other's territory. (C.T. Cape Town, K. Knysna, P.E. Port Elizabeth, E.L. East London, D. Durban, B. Beira, Z. Zanzibar, V.F. Victoria Falls)

By Courtesy of Piscator

From a study of water temperatures and habitats it is quite clear that these do not govern the distribution of *A. nebulosa labiata* and *A. mossambica* over a river system. The elver zone of *A. mossambica* has been defined above as lying between Lat. 21° S. and Lat. 31° S. and by comparing this with the known distribution inland of *A. mossambica* it becomes apparent that the governing factor is the size of the eel reaching the river mouths lying within this zone. It is quite clear that this principle is applicable to the distribution of *A. nebulosa labiata* in the rivers of Kenya, and can, in fact, be extended southwards to the Zambezi and Pungwe Rivers. An elver zone for *A. nebulosa labiata* can be defined therefore as lying between the equator and 21° S. These elver zones are the areas along the east coast where all available

evidence points to the arrival of true eiders of the species *A. nebulosa labiata* and *A. mossambica*.

Frost (14) also described eiders of *A. bicolor bicolor* from Dar-es-Salaam. The southerly limit of the eider zone of *A. bicolor bicolor* is not known, but it is significant that specimens of *A. bicolor bicolor*, as small as 149 mm., were collected in the Lundi River, Southern Rhodesia, at a site 190 miles by river from the sea, an unusual distance inland for this littoral species to be found.

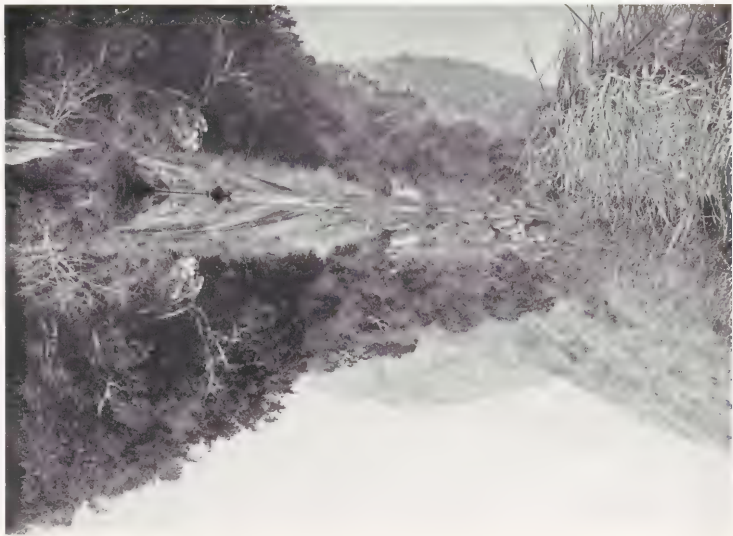
No eiders of *A. marmorata* have been discovered along the east African coast so far: the only records come from Madagascar. In South Africa this species has been found in the deep pools of the lower reaches of rivers only, and in many cases anglers take large specimens at the ebb and flow of the tidal sections of these rivers. It is only north of the Limpopo River that this species is found any distance inland. In Southern Rhodesia *A. marmorata* were taken at a site on a tributary of the Lundi River 250 miles inland. Frost (9) reports one eel, undoubtedly *A. marmorata*, from above the Lusemwa Falls, 630 miles from the sea. Ege (3) quotes Herre as giving one of the localities for *A. marmorata* as the mountain streams up to altitudes of more than 1,530 metres (5,000 ft.), whereas Bertin (15) states: "...*A. marmorata* and *A. megastoma* are on the contrary eels with long dorsal fins and speckled dress which harmonises with the pebbly bottom of inland waters: rivers of the plains for the first, mountain torrents for the second." It would appear that even *A. marmorata* can tolerate a wide variety of habitats, and that its distribution inland is also related to the size of the eel reaching the river mouth. The mouth of the Zambezi River falls within the zone from which Jespersen (18) described larvae of this species.

In studying the distribution of eels over a river system two more factors governing the ultimate dispersal over a system have become evident: the permanency of river flow, and the nature of an obstruction in relation to the distance by river from the sea.

When Livingstone discovered Lake Nyasa in 1859 the Shire River was flowing, and it can be assumed that a reasonable discharge was taking place from this sole outlet of the lake. It is not known when the water actually stopped leaving the lake, but certainly there was no flow in 1914 when the lake level reached an absolute minimum. From that date the water level gradually rose and it was not until 1934 that the flow from the lake was re-established, and a maximum level recorded in 1940. During this period mature eels must have left the lake or perished in the attempt, and as no small eels were able to enter the eel disappeared from the fish fauna of the lake. That *A. nebulosa labiata* was found in Lake Nyasa prior to 1925 is recorded by Ege (3) and Schmidt (43). It was not until 1954 that *A. nebulosa labiata* (11) was again recorded from Lake Nyasa.

Further inland, approximately 600 miles, Frost (9) records *A. nebulosa labiata* together with *A. marmorata* from above the Lusemwa Falls, approximately 630 miles upstream from the mouth of the Zambezi River. The same distance from the sea we find the Kafue River Gorge with its waterfalls, and here no eels have been able to negotiate them. Further inland still, 900 miles from the Indian Ocean, the Victoria Falls, with a height varying from 200 feet at the western end to 323 feet at the eastern end, have proved an impassable barrier to eels and they are absent from the huge catchment of the Upper Zambezi River. *A. nebulosa labiata* is found in the gorge below the Victoria Falls and tributaries of the Zambezi River as far as 1,100 miles from the Indian Ocean. Neither the Victoria Falls nor the waterfalls of the Kafue Gorge are more formidable in height than the Howick Falls, Tsitsa Falls or Tina Falls which have been mounted by *A. mossambica* in South Africa. It would appear therefore that by the time young eels reach the Kafue Gorge they are too large to negotiate these particular waterfalls, and that physical conditions are quite unsuitable for an overland route.

That the waterfalls of the Kafue Gorge should be an insurmountable barrier to the up-



View of the Umzimkulwana River, Orbi Gorge.

stream migration of eels is of considerable interest. Only a short distance above the confluence of the Kafue and Zambezi Rivers, and set in similar physical surroundings, we find the mighty 420-foot concrete wall of the world's largest man-made lake, Lake Kariba. With a catchment area of some 56,000 square miles below the Victoria Falls, the population of eels above the wall must be considerable. Should the wall of Lake Kariba prove impossible for young eels to negotiate, as well it may, then the species *Anguilla* will disappear from the Zambezi River system above it.

Skead's (24) detailed observations of eels mounting obstructions, whilst migrating up the Buffalo River, show that most eels between 10.0 and 20.0 cm. in length have little difficulty in mounting a spillway such as that of the Laing Dam, which is 108 feet high, provided there is water coming over the spillway. Droughts and the lack of a permanent flow of water in a river have a great influence on the distribution of eels in a particular river system. The Van Ryneveldt's Pass Dam just north of Graaff-Reinet, which has frequently been dry of recent years, has not overflowed since 1933. Eels are now entirely absent from the Sundays River in this area, but old residents can remember when they were caught near the town. North of George the Doring River, which is a tributary of the Gourits River, was found flowing strongly in September, 1958. A selected section was treated with rotenone and found to be populated with *Barbus asper* only, no *Anguilla* were found. The caretaker of the Kammanassie Dam, also on the Gourits River system, said that in the eighteen years he had been there he had not heard of an eel being caught in the dam. In both cases the lack of flow of water in the Olifants River and Gourits River below had decimated the eel populations of that part of the river system. The same story holds for the Grassridge Dam and Lake Arthur on the Fish River system. Once an eel population is wiped out by drought it takes many years before sizeable eels become apparent to the angler.

As stated above, all available evidence points to the fact that the distribution over a river system is related to the size of the eel entering the river mouth. Occasional eels have been found in the Orange-Vaal river system (13) and those examined have been *A. mossambica*. Although the mouth of the Orange River is within the range of stray *Anguilla* passing round the Cape coast, it is considered that eels reaching this point and migrating up the Orange River would be too large to negotiate the Aughrabies Falls. These waterfalls are 480 feet in height and physical conditions in the area are quite unsuitable for any overland migration. On the other hand in the Heidelberg-Bethal-Ermelo area of the Transvaal highveld the tributaries of the Vaal River lie close to the headwaters of tributaries of three large systems, the Limpopo, Komati and Pongolo Rivers, all of which enter the Indian Ocean within a known elver zone of *A. mossambica*. We can therefore expect this species to make the deepest penetration up these rivers, and occasional small eels to cross the low-graded watershed during the rainy season and reach the Vaal system.

LENGTH-WEIGHT CURVES FOR *A. marmorata*, *A. nebulosa labiata* AND *A. mossambica*

Including data published by Frost (10) for *A. nebulosa labiata*, a length-weight diagram (fig. 15) has been prepared from material collected for the species *A. marmorata*, *A. nebulosa labiata* and *A. mossambica*. The number of specimens of *A. marmorata* is limited but throughout their range in size they have been found to be heavier than the other two long-finned eels. The curve for *A. mossambica* shows a distinct rise above 100 cm., this is due to the fact that all the specimens greater than 100 cm. in length were mature females with enlarged gonads. From Frost's (41) work a curve for *A. anguilla* would fall between those of *A. mossambica* and *A. nebulosa labiata*, and the average range in length would be less than that of *A. mossambica*. *A. nebulosa labiata* grows to a considerable length and weight, and unidentified eels whose weights have been stated to be between 40 and 50 lb. would almost certainly have been *A. marmorata* or *A. nebulosa labiata*. Schmidt (43) records a giant specimen of *A. nebulosa labiata* from Lake Nyasa whose head alone weighed 2½ lb.

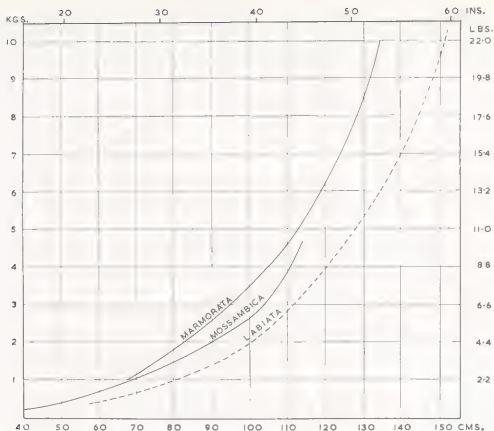


Fig. 15. Length-weight curve for the three long-finned eels.

PERIOD SPENT IN FRESH WATER

Working on fresh material from the eel fisheries on Lake Windermere and the River Bann, Frost (35), (40), by reading the otoliths, was able to establish that the males of *A. anguilla* stayed in fresh water 6 to 10 years, and the females 9 to 19 years. Although no mature eels of the species *A. nebulosa labiata* were found in Kenya waters, Frost (10) found that males of this species had been in fresh water 6 to 8 years, and females of 100 cm. to 128 cm. 10 to 19 years. Unfortunately otoliths removed from specimens preserved in formalin have been found to be quite unsuitable for reading. To use Frost's technique it will be necessary to remove the otoliths from freshly killed specimens, thoroughly clean them in absolute alcohol and preserve them in a normal saline solution to which a little lysol has been added. When further material has been examined it will most likely be found that *A. mossambica* follows the general trend shown by examination of the otoliths of *A. anguilla* and *A. nebulosa labiata*, and that the males stay in fresh water 6 to 10 years before reaching maturity, and the females 10 to 19 years. On length alone, the 135 cm. female *A. nebulosa labiata* from the Marble Hall Research Station in the Transvaal would have been approximately 17 years

in fresh water, as compared with *A. nebulosa labiata* of a similar length from Kenya waters.

From his work on larval eels collected in the Indian Ocean Jespersen (18) came to the conclusion that the larvae of the inter-tropical eels have a much shorter pelagic life than the larvae of *A. anguilla*; whereas the larvae of the latter species have an extended larval life of nearly three years, those of inter-tropical eels take less than a year to reach the metamorphosing stage. This naturally has some effect on the characteristics of the otoliths and has been illustrated by Frost for *A. nebulosa labiata* (fig. 16). Working on the otoliths of

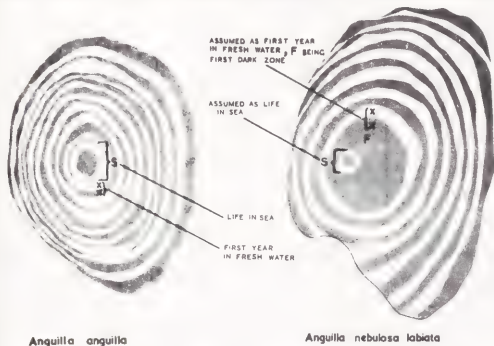


Fig. 16. After Frost

elvers of *A. mossambicu* from the mouth of the Uvongo River both Frost and Talbot have found these to have a minute opaque nucleus surrounded by a translucent zone with a narrow opaque peripheral ring. As these elvers were taken as they were leaving the sea this must represent the life at sea, and is slightly less than the area "S" assumed by Frost to represent the life at sea spent by larval *A. nebulosa labiata*. The otoliths of post-elvers from the Laing Dam wall were found to have the opaque nucleus, translucent zone, distinct opaque band, and then a wide peripheral translucent zone similar in detail to the zones marked "S" and "F" in fig. 16 for *A. nebulosa labiata*. As the life-history of the Laing Dam post-elvers is still being studied it is not possible, at present, to say whether or not the wide peripheral translucent zone was laid down during a secondary migration at sea, or in fresh water.

POPULATION TESTS AND FEEDING HABITS OF THE EELS

Where conditions made it possible rotenone powder was used for population tests. Although the results of these are valueless for the determination of the productivity of a

large river or inland water, their composition is of interest and the general trend applicable. The percentage frequency of lengths of eels collected in two tests, carried out on the Kariëga and Kromme Rivers respectively, is shown in fig. 17. This trend is evident throughout the Eastern Cape, Natal and Rhodesia, i.e. a few large eels in a likely pool, together with an increasing number of small eels. In the two cases graphed in fig. 17 the drop in percentage frequency at the 40 to 50 cm. range is associated with the number of male eels found in these areas. The entire populations were *A. mossambica*.

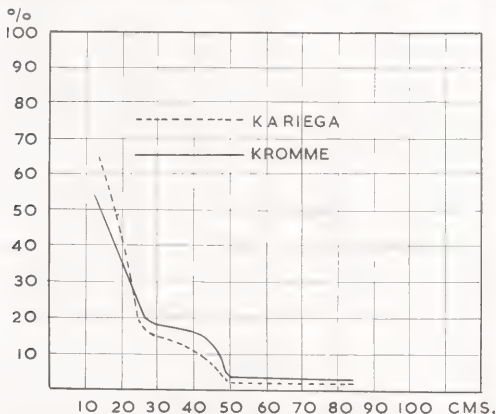


Fig. 17. Population tests made from random pools in flowing river. Percentage frequency of size. Kariëga 93 specimens, Kromme 125.

Throughout this investigation the eels collected have been dissected and their stomach contents examined. A histogram (fig. 18) has been prepared from this data which covers post-elvers, feeding eels and mature eels of all species. The histogram, arranged in groups with lengths of 10 to 20 cm., 20 to 30 cm., etc., shows a marked change in diet after attaining a size of about 20 cm. From about 50 cm. onwards the aquatic larvae and nymphs of insects virtually disappear from the stomach contents and the main diet becomes small fish, crabs and an occasional frog. The larger the eel, the larger the animal preyed upon. Apart from preying upon trout, the eel, throughout its life in fresh water, is a competitor for food in trout streams. Many small eels have been found engorged with *Simulium* larvae. It is interesting

to compare fig. 17 and fig. 18 and realise how well the available food supply in an individual pool is made use of by the eels populating it. The large eels always have food, even if they have to resort to cannibalism.

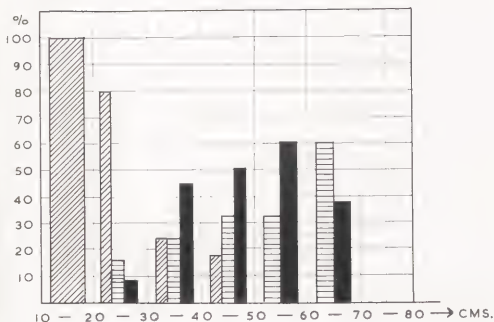
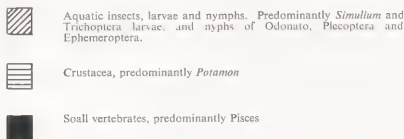


Fig. 18. Histogram showing size of *Anguilla* and percentage frequency of stomach contents

PARASITES

Macroscopic examination revealed three species of internal parasites, all Nematode worms. By far the most common were those found in the stomachs of *A. mossambica*, fig. 19, from the Buffalo River. Samples of these sent to the British Museum were very kindly identified by Mr. W. G. Inglis as *Ortleppina longissima* (Ortlepp), 1922. Nothing is known of the life-cycle of this Nematode worm, but as it appears in the stomachs of eels less than 20 cm. in length, it would appear that an intermediate host could be the aquatic nymph or larvae of an insect. Although eels from the Buffalo River and the Kei River were infested those of

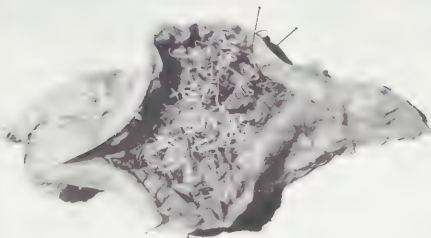


Fig. 19. Stomach of *A. mossambica* from the Buffalo River, E. Cape, showing nematode parasites.

the Kariëga River and rivers round the coast to Knysna have been free of this particular parasite. Of the eels collected in Southern Rhodesia none was infected.

SECOND METAMORPHOSIS: YELLOW EEL TO SILVER EEL

The first mature eels to be recorded in South Africa were those collected by Professor Omer-Cooper of Rhodes University. On the night of 1st February 1953, eels were found crawling over the sandbar at the mouth of the Kleinemonde River towards the sea. Four specimens were collected; two of these 44.0 cm. and 43.2 cm. total length, were sent to the British Museum (10), one of 45.0 cm. to the Department of Ichthyology, and a specimen of 42.0 cm. to the South African Museum (29). All these proved to be male *A. mossambica* with well-developed gonads. The enlarged eyes and pointed snouts were typical of silver males of *A. anguilla*. The South African Museum has two more specimens, S.A.M. 12128 from the Transvaal, and S.A.M. 13423 from Zululand, Natal. The Kaffrarian Museum submitted a specimen of 47.0 cm. taken from the Laing Dam, December 1956. In the field a specimen of 43.5 cm. was taken from the Kariëga River, November 1957, and 9 specimens 34.5 cm. to 51.5 cm. were taken from the Kromme River during the same month. Particular note was taken of the colour of these specimens: the dorsal surface was very dark bronze, the flanks shaded to iridescent light bronze, and the belly was silvery white. Collected at the same time were males which were obviously undergoing metamorphosis. These were slightly lighter in colour, more like the yellow eels, but the marked difference was the enlarged eye and pointed snout. The mature male *A. mossambica* from the Kromme River, with their enlarged eyes, pointed snout and well-developed gonads, dark dorsal surface and silvery white belly, were typical silver male *A. mossambica* when compared with descriptions of silver male *A. anguilla*, but all had been feeding and there was no sign of degeneration of

the gut. On the 14th March, 1959, Mr. P. McGahey found eels trying to leave the Kleinemonde River mouth and he collected a silver male *A. mossambica* of 43.0 cm. Mature male *mossambica* of 34.5 cm. to 51.5 cm. in length, and a range of 110 grams to 300 grams in weight, have been found during the months November to March.

The first mature female of this species came from Mrs. L. Jolly of Kasouga (30), where it was captured on the 16th November, 1957, as it was leaving the estuary for the sea. When alive, the dorsal surface was metallic black with iridescent sheen; the dorsal, caudal and posterior half of the anal and pectoral fins were the same colour. On the flanks the dorsal colouring blended through sea-green and sky-blue iridescent shades to silvery white belly with pale pink iridescence, rather like mother-of-pearl.

This eel weighed 3 lb. 2 oz., and had a total length of 77.5 cm. and a girth of 20 cm. When laid out flat the gonads had a maximum width of 3.9 cm. These were full of minute blood vessels giving them a general pinkish colour in contrast to the very white opaque gonads of large females approaching maturity. The egg-cells were at a stage where they were as large as 0.25 mm. in diameter, with a nucleus of 0.076 mm. In catadromous eels of the species *A. japonica*, Matsui (31) found the egg-cells to vary from 0.17 mm. to 0.27 mm. in diameter, and the nucleus diameter to vary from 0.056 mm. to 0.084 mm.

Additional material covering the period mid-October to mid-March was obtained: the largest female was 114.0 cm., weighed 10 lb. 4 oz. and had gonads 5.0 cm. wide. In all 14 of these the gonads were streaked with minute blood vessels. Of particular interest were two mature female *A. mossambica* found by Mr. Uys, caretaker of the Laing Dam, at the base of the spillway. These eels were apparently involved in a downstream migration to the sea and came over the spillway on the dry side, and were killed on the rocks 108 feet below. These eels, of 103.0 cm. and 6 lb. in weight, were found on the 16th of March, 1959, two days after an attempt by mature eels to leave the Kleinemonde River was observed by Mr. P. McGahey.

Mass migrations of mature eels on a scale witnessed in western Europe have not been observed in South Africa, but that these take place in Natal is shown by the fact that during November the 30-inch main from the Shongweni Dam, which supplies Durban with some of its water, is occasionally blocked by migrating eels and they have to be cut out in chunks (27). Of those mature female eels found during November to March, the body colours resemble greatly the published descriptions of silver female *A. anguilla* (15), and silver female *A. japonica* (31). Of the material examined the size of the silver female *A. mossambica* ranges from 77.5 cm. to 114.0 cm. and a weight of 1.1 Kg. to 4.65 K (3 lb. 2 oz. to 10 lb. 4 oz.). Silver female *A. mossambica* from this limited material are larger than silver female *A. anguilla* and *A. japonica* but the males of all three species fall within the same range. The largest male *A. mossambica* collected was 51.5 cm. and the smallest female 77.5 cm.; therefore in silver *A. mossambica* all those smaller than 55.0 cm. are most likely to be males, and all those greater than 70.0 cm. females.

One of the outward distinguishing features of the eel approaching maturity, or undergoing metamorphosis, is the enlargement of the eye, the diameter of which may be as much as doubled. Carlisle and Denton have studied the metamorphosis of the visual pigments of *A. anguilla* (32) and found that when *A. anguilla* assumes the silver livery of approaching maturity, the eye enlarges and the retina changes from a purple colour to a golden colour, like that of the chrysopsins of deep-sea fish. This change takes place even before the fish leaves fresh water. The larger eye, and relatively even larger pupil of the silver eel make it a more efficient light-collecting organ, whilst the total retinal density of photosensitive pigment is higher in the silver eel than in the yellow eel, and the retina will therefore be more efficient in usefully absorbing the light incident on it. Field notes made of the live colours of *A. mossambica*, both yellow and silver eels, show that the retina pigments respectively are the

same as those of *A. anguilla*, and, as stated above, the enlargement of the eye takes place in fresh water. The heads of a typical silver male *A. mossambica*, and silver female, are shown in figs. 20 and 22.

On the 25th of February, 1958, a mature female *A. marmorata* was collected in the Sundays River near Addo, approximately 18 miles above the ebb and flow. This eel weighed 22 lb., the total length was 134.0 cm. and the gonad width 5.1 cm. The pointed snout and gonad development can be seen in figs. 24 and 25. In colour this was also a silver eel, the dorsal surface being uniformly dark, and the belly silvery white with iridescent mother-of-pearl tints. The characteristic mottled pattern of this species was evident along the flanks. The pointed pectorals shaded from jet black posteriorly, through dark purple to silvery white. The retina of the eye was golden, but the change in retina pigment is not as marked in this species as the retina of the yellow eel tends to be olive, the predominating light colour of both *A. marmorata* and *A. nebulosa labiata*.

A large silver female *A. nebulosa labiata* was trapped in a fish pond at the Marble Hall Research Station of the Transvaal Provincial Fisheries Department, and was forwarded for

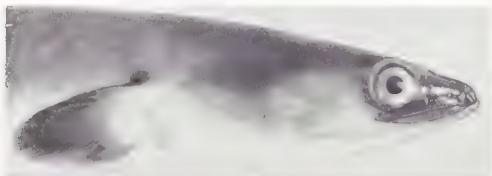


Fig. 20. Head of male silver eel, *A. mossambica*, 51.5 cm. (about 20 inches) from Kromme River, November, 1957. Note pointed snout and large eye.
(Photos: R. A. Jubbs)

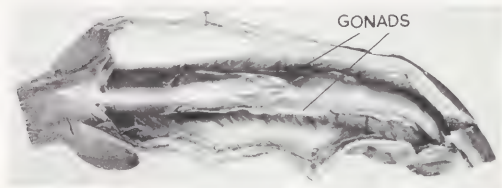


Fig. 21. Gonads of male silver *A. mossambica*

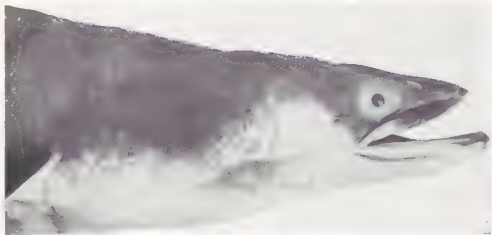


Fig. 22

(Photo: R. A. Jubb)

The head of female silver eel *Anguilla mossambica*, length 40 inches, weight 6 lb. This shows the large eye and pointed snout. This specimen was one of some which unwittingly committed suicide in trying to go downstream from the Laing Dam on the Buffalo River. They went over the spillway and crashed onto the rocks below, where they were found by Mr. P. F. Uys, Supervisor of the dam, in March 1959

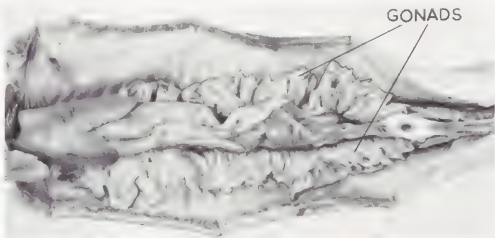


Fig. 23. Gonads of the Kasouga River silver female eel. The gonads extend well posterior of the anus.

examination. The large eyes, pointed snout and pectoral fins, together with enlarged gonads, showed this to be a mature female. This specimen had a total length of 135.0 cm. and weighed 16 lb. The site where this eel was captured is approximately 375 miles from the Indian Ocean. A male *A. nebulosa labiata* of 59.0 cm. was collected by R. Bolt near Chirundu, Zambezi River, in September 1959. This eel, with its enlarged eyes and gonads, and the pointed



Fig. 24. Head of a large mottled eel *Anguilla marmorata* from the Sundays River. Note large eye and pointed snout of the mature female.

(Photo: R. A. Jubbs)



Fig. 25. Gonads of silver *A. marmorata*

snout of the mature eel, was probably preparing to migrate downstream with the seasonal floods of December and January. As this site is 600 miles from the sea, it is of great interest to realise just how far inland this final metamorphosis starts. Neither of the above two speci-

mens was seen alive, but the preserved specimens are very dark on the dorsal surface, with light belly and mottled pattern on flanks.

During ploughing operations in a swamp near the Umfolozi River, Zululand, in September 1957, Mr. L. van Heerden captured a female *A. bicolor bicolor* of 64.0 cm. and 1 lb. 2 oz. in weight. The width of the gonads was 1.2 cm., the eyes enlarged and the snout pointed. In contrast to the usual olive colour the dorsal surface was uniform bronze and the belly silvery. Like all the other specimens of mature *Anguilla* found in South African rivers, this eel was still feeding.

From material collected and received for examination it is evident that eels in South African rivers undergo metamorphosis from the yellow eel to the silver eel during the period September to December, and that mature silver eels can be found during the months November to March. In this regard it should be noted that catadromous eels are common in England and Ireland during the months October to December, in Italy October to December, and Japan September to January. If, as is generally accepted, the mature eel requires rivers in flood to facilitate its journey to the sea, then along the coast from the Zambezi River to East London we can expect maximum activity during the rain months January to March.

HYPOTHETICAL BREEDING GROUNDS OF THE EELS WHOSE ELVERS REACH SOUTH AFRICA

Of the five species of eels of which adults have been found, the elvers of three, *A. nebulosa labiata*, *A. mossambica* and *A. bicolor bicolor* are known to reach the East Coast of Africa. The elvers of a fourth species, *A. marmorata*, are known from Madagascar and larval eels from the vicinity of Madagascar and the East Coast of Africa have been described by Jespersen (18). Thus four distinct species, either as elvers or as larval eels, can be found along, or adjacent to, the east coast during the same seasonal period. By their very nature the leptocephalids of these species would be carried towards Madagascar and Africa by the South Equatorial Current. This, as is shown in fig. 26, is split by the island of Madagascar, part going round the northern tip and part going round the southern tip. The flow round the northern tip splits again, part curling northwards and becoming the East African Coastal Current (33), and part curling southwards through the Madagascar Channel where it is known as the Mozambique Current whose warm water sweeps the coast of Portuguese East Africa and Natal. The flow round the southern tip of Madagascar curls slightly north-west before joining the Mozambique Current and flowing south-west as the Agulhas Current. This combined current of warm water flows southwards along the coast of Natal and Pondoland, but south of Port St. Johns the picture becomes complex. Counter-currents of relatively colder water are found close inshore, and the warm Agulhas Current continues southwards as an off-shore current until it reaches the Agulhas Bank. According to Clowes (34) this obstruction causes a deflection to the south-west of the greater part of the Agulhas Current, but a further obstruction is encountered in the presence of the eastward-flowing water of the South Atlantic Ocean. This causes the main part of the Agulhas Current to be bent back on itself and flow towards the east, being now known as the return Agulhas Current. Although the main part of the Agulhas Current is deflected as stated, and eventually returns eastwards to the South Indian Ocean, it is also a fact that a small part of the current flows both over and round the Agulhas Bank.

The current flows in fig. 26, which has been extended to fit the known distribution of elvers and larval eels, give a broad picture of prevailing conditions during January and February. As it is during these months that cold in-shore counter-currents are common along the south-east coast, these have been marked in. Jespersen (18) has shown that a likely breeding place for *Anguilla* species in the Western Indian Ocean could be found east of Madagascar between 10 S. and 20 S., and between 60 E. and 65 E. Assume that *A. mossambica* used the southerly portion of this hypothetical breeding area. The bulk of the larvae would then be carried on the southern periphery of the South Equatorial Current, and larvae

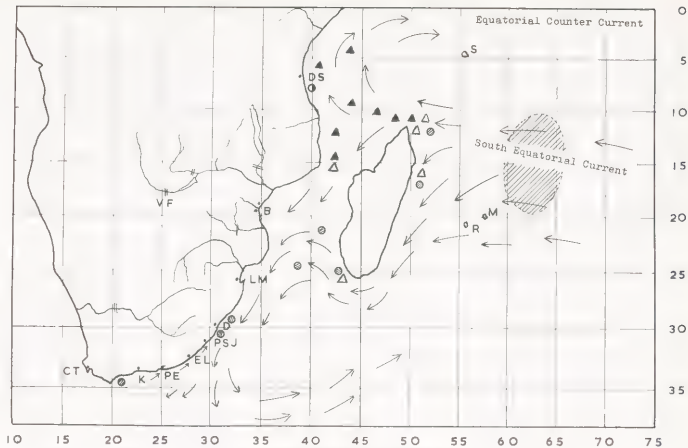


Fig. 26. Prevailing ocean currents with distribution of elvers and larval eels during the period December to February.
Hatched area hypothetical breeding ground

- $\triangle$ *A. marmorata*
- $\odot$ *A. nebulosa labnata*
- $\otimes$ *A. mossambica*
- $\blacktriangle$ *A. bicolor bicolor*
- $\parallel$ Significant waterfalls or cataracts

and elvers would reach the east and south-west coasts of Madagascar, as well as the coast of Portuguese East Africa south of Lat. 21 S., and Natal. With the prevailing Agulhas Current swinging away from the coast south of Port St. Johns, and due to marked phototaxis and thermotaxis (15), current-carried larvae would tend to align themselves with the warm water and be carried past the south-east coast towards the Agulhas Bank. Here, according to prevailing conditions, some pass westwards, but the majority swing eastwards in the return Agulhas Current. In both cases it is considered that metamorphosis is completed.

Strubberg (26) has shown that metamorphosis is accelerated by high water temperatures and retarded by low temperatures. The Breede River specimen of *A. mossambica*, S.A.M. 19851, of 51.0 mm., is proof that some larval eels are carried westwards, and its size may be associated with ambient water temperature. Just what happens to those post-elvers carried into the South Indian Ocean is pure conjecture, but it is thought that these remain at sea feeding and growing until they reach a size at which they are capable of stemming the current and reaching the mainland. It is probable that these are the post-elvers that reach the rivers of the south and south-east coasts, between Knysna and the Kei River mouth, and populate them. Like their adults, tendencies towards thermotaxis disappear once metamorphosis is completed.

From the known elver zones and distribution of larvae, it seems likely that the northern section of this hypothetical breeding ground is used by *A. marmorata*, *A. nebulosa labiata* and *A. bicolor bicolor*, and the bulk of the larvae carried in the northern periphery of the South Equatorial Current into the East African Coastal Current and the northern part of the Mozambique Current. If this hypothesis is correct then it is difficult to understand why *A. nebulosa labiata* is absent from the rivers of Madagascar. If future collections of eels from Madagascar show that this is indeed the case, then *A. nebulosa labiata* either breeds close to the coast of East Africa, or its larval life is a prolonged one. In this latter case, as propounded by Tucker (16), larval environment may account for the mean vertebral count of 111 which separates this species from *A. nebulosa nebulosa* which has a mean vertebral count of 109, and they may actually originate from the same spawning area.

Therefore, as suggested by Jespersen (18), a breeding ground east of Madagascar for the species *A. marmorata*, *A. mossambica* and *A. bicolor bicolor* is highly probable. Not only does such a site favour the dispersal of larvae in the South Equatorial Current, but also it is within reasonable distance of Madagascar and the East Coast of Africa for mature eels to return for breeding purposes. As stated before, there is evidence of considerable wandering around in the sea by post-elvers after metamorphosis, and this could account for the specimen of *A. obscura* found in the Buffalo River, near King William's Town.

EXPLOITATION OF FRESH WATER EELS

The prevailing price in Cape Town of smoked eels imported from Holland is R1.45 a pound. Danish eel cutlets, in small tins, sell at R0.62 a tin, and in Pretoria Japanese processed eels can be bought for R0.48 a tin whose contents weigh 3½ oz. From advertisements in the Press offering special eel dishes there certainly appears to be a demand for smoked or processed eel flesh. In addition to this there is a big demand for flesh of high protein value, which in the case of the eel ranks with that of fowl flesh and is slightly higher than that of beef. In South Africa, where there are eels in the rivers, it has been found that there are ardent eel anglers of all races who fish for eels for their own consumption; in conversation all those anglers who have been interviewed declare that eel flesh is a delicacy.

In Europe eel fisheries operate by intercepting the catadromous mature eels as they leave large inland waters for the sea. One of the largest commercial eel fisheries operates on the River Bann, which empties Lough Neagh, a lake of 153 sq. miles in Northern Ireland. Another extensive eel fishery operates at the mouth of the 125 sq. mile Commachio lagoon

in Northern Italy. It is these large inland waters with their single outlets that provide the most economical way of cropping the eel populations. This is done by a system of weirs and traps right across the river. The effects of floods are cushioned by these expanses of water. To ensure that eel populations are maintained, elvers migrating annually from the sea are intercepted in simple but efficient traps (35) and transported to the inland waters. From both Ireland and England elvers are exported annually to Holland and Germany for stocking rivers and dykes.

In South Africa there are no inland waters comparable in size with those of western Europe. It is only in the larger and more permanent rivers flowing into the Indian Ocean that we can expect to find eel populations that can be continuously exploited. But due to floods, which usually carry the mature eels to the sea, permanent eel weirs would be a problem. Large dams assist, not only in providing living space for eels, but also in cushioning the effects of floods, and it is at the exits of these that eels could be trapped. The proviso is, of course, that the dam is of a fairly permanent nature, and elvers can reach it. Dam walls near the sea provide an excellent site for trapping elvers or post-elvers for stocking inland waters, and the Laing Dam wall on the Buffalo River is such a site. Experiments have been carried out which show that post-elvers can be transported by organised transport from this site to any major river system in the Cape Province, Orange Free State and Natal.

The largest river system in the Union is the Vaal-Orange which very few eels reach. Some of the rivers of the Transkei and Natal, with their deep meandering channels near the sea, provide large volumes of water which harbour hordes of eels. The Bashee River has long been famous for its eels and it is north of this that the first and only eel fishery in South Africa operated.

In 1949 Mr. G. Hylton-Gardiner (36), after preliminary investigations, decided to establish a commercial eel fishery in the Humansdorp area. He brought an expert eel trapper, Mr. B. P. de Kriek, from Holland and operated on the Kromme and Gamtoos Rivers. An eel smokery was established at Humansdorp, and as the product compared very favourably with that imported from Holland he was able to dispose of all that could be produced. These two rivers did not contain eel populations sufficient to stand exploitation and supplies diminished. Knowing the Transkei rivers Gardiner moved to Umtata in early 1950. In this area eels proved to be plentiful and again he had no difficulty in disposing of the processed catch commercially in East London. Unfortunately Gardiner died in May 1950, and with him the initiative for this venture, as well as a scheme he wished to organise for harvesting eels in the Transkeian rivers, from which Natives would benefit financially as collectors.

For the catching of large eels de Kriek used Dutch "fuik" nets and baited hand-lines, the latter proving more efficient. During this investigation it has been found that night lines, baited with fresh *Barbus* or *Labeo*, were more efficient for catching eels than "fuik" nets or baited eel traps of wire-netting as used in New Zealand (37). Electrical methods, which have proved efficient in New Zealand (38), have not been used. Where eels can be cropped in mass migrations properly constructed weirs of nets and traps would be the most economical and efficient way of cropping eels, but in South African rivers this is not feasible except in the vicinity of large storage dams. The more large inland waters there are, the greater will become the possibility of cropping eels efficiently in rivers where they are numerous. There are no stocking problems to contend with as each year the sea provides millions of healthy young eels which could support a large industry if they had water in which to feed and grow.

ACKNOWLEDGEMENTS

I am indebted to Professor J. L. B. Smith of the Department of Ichthyology for proposing this interesting investigation, and to the Council for Scientific and Industrial Research, Pretoria, for a generous grant which enabled me to carry out field work covering the rivers of South Africa from the Cape to Southern Rhodesia.

A more opportune time to initiate this project could not have been chosen as much interest in the freshwater eels had been stimulated by the writings of Mr. A. C. Harrison, Editor of *Piscator*, the Journal of the Cape Piscatorial Society. As will be seen in the list of references Mr. Harrison has shown a keen interest in this work, and he has very kindly loaned some half-tone blocks for illustrating this paper.

In 1948 Dr. Winifred Frost of the Freshwater Biological Association, England, an authority on the European eel, spent six months in Kenya studying the biology of the eels of Kenya rivers. I have been fortunate in having at my disposal her published works and collaboration in an investigation which still has many puzzling problems to solve.

Mr. J. Skead, Director of the Kaffrarian Museum, started his observations on the migrations of eels up the Buffalo River in 1955, and he has very generously placed his data and material at my disposal, and has guided me to excellent collecting sites in his area. In their respective areas Mr. F. Talbot of the South African Museum, and Mr. R. Liversidge of the Port Elizabeth Museum have been most co-operative in providing technical assistance and material.

I wish to thank the Directors and Fish Research Officers of the Department of Nature Conservation, Provincial Fisheries Institute, Lydenburg, and the Natal Parks, Game and Fish Preservation Board for assistance and specimens.

In the field valuable material has been collected and forwarded by Messrs. Terence Larkin and E. Drower who intercepted migrations of elvers up the Uvongo Falls; Mr. Byrne of Shongweni Dam, Natal, who intercepted a secondary migration of post-elvers up the Shongweni Dam wall; Mr. Uys of Laing Dam who collected two silver female *A. mossambica*; Mrs. L. Jolly who intercepted a silver female *A. mossambica* leaving the Kasouga River; Dr. Stewart for specimens of *A. mossambica* from the Haenertsburg trout streams, and Mr. R. Bolt for specimens of *A. n. labiata* from the Zambezi. Mr. P. McGahey intercepted a silver male *A. mossambica* which was leaving the Kleinemonde River for the sea.

Through the courtesy of the Conservator of Forests, and the Municipalities of East London, King William's Town, Port Alfred, Grahamstown, Port Elizabeth and George, I was granted access to rivers and storage dams not normally frequented by the public.

My thanks are due to Mrs. M. M. Smith of the Department of Ichthyology, Dr. R. F. Ewer and Dr. McCallan of the Department of Zoology for technical assistance, and to my wife for the illustration of *Anguilla nebulosa labiata* and permission to publish it.

Dr. T. H. Barry, Director of the Albany Museum, has very kindly arranged for the publication of this paper. The two plates have been sponsored by the Council for Scientific and Industrial Research, Pretoria.

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